

are still in flux. The Euciliata, advancing from this condition, have become stereotyped in a definitely binucleate state with secondary nuclear specialization.

Classification of Ciliata
 Protociliata
 Opalinidae
 Protoopalina
 Opalina
 Euciliata

ZOOLOGY.—*Synopsis of the supergeneric groups of Rodents.*¹

GERRIT S. MILLER, JR., and JAMES W. GIDLEY, U. S.
 National Museum.

Work on the taxonomy of the Rodents, living and extinct, has occupied much of our time during the past four years. This paper contains a brief synopsis of the results.

The classification which we have adopted is based on the following conception of the evolutionary course followed by the order during its development. This course has been mainly conditioned by the mechanical problem of strengthening a chewing apparatus in which the unusually important cutting function of the incisors is strongly contrasted with the grinding function of the cheekteeth; the highest degree of efficiency to be given always to the incisors and in most instances to the cheekteeth as well. The problem has been solved by five sequences of correlated changes in the masseter muscle and the bones to which this muscle is attached. All of these sequences could originate from the structures present in a generalized mammal, but there is no evidence that any rodent during its development has passed from one to another. The groups characterized by the various sequences are therefore natural. We have treated them as superfamilies: the *Sciuroidae*, *Myoidae*, *Dipodoidae*, *Bathyergoidae*, and *Hystrioidae*. Of the secondary problems the most conspicuous has been the strengthening of the cheekteeth. These teeth, however unlike their structure in extreme instances may appear, have all been developed from some primitive, low-crowned, tritubercular type not essentially different

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from that present in the Eocene *Paramyidae* and in living species of *Sciurus*. During the adjustment of the cheekteeth to increasingly heavy fore-and-aft grinding motion, a process which has taken place in most members of the order, the crown height has been augmented, while the original tubercles and lophs have been made more efficient by (a) increase in complexity, and (b) conversion into transverse ridges and specialized enamel plates, usually with reduction in the number of elements present. In each superfamily the characteristic modifications in the muscles and skull were begun in connection with the development of the incisors. Mechanical improvement of the cheekteeth came later. All rodent teeth have been developed from an essentially uniform original type under the influence of practically identical mechanical forces. Parallelism in highly specialized dental structures between genera and species which are not closely related is therefore frequent enough to be one of the noticeable peculiarities of the order. The history of development extends so far into the past that the essential features of structure are modernized in the oldest known Eocene rodents. No extinct member of the order has yet been found which can be regarded as ancestral to any considerable number of subsequent forms.

The order *Rodentia* may be defined as follows: Terrestrial and fossorial (occasionally arboreal or semiaquatic) placental mammals with both brain and placentation generalized in type; feet unguiculate; elbow joint always permitting free rotary motion of forearm; fibula never articulating with calcaneum; masseter muscle highly specialized, divided into three or more distinct portions having slightly different functions; cecum without spiral fold; dental formula not known to exceed $i \frac{1}{1}, c \frac{0}{0}, pm \frac{2}{2}, m \frac{3}{3} = 22$ permanent teeth; incisors scalpriform, growing from persistent pulp, the enamel of the upper tooth not extending to posterior surface; distance between mandibular and maxillary toothrows approximately equal, both pairs of rows capable of partial or complete opposition at the same time, the primary motion of the lower jaw in mastication longitudinal or oblique.

Superfamily SCIUROIDAE

Masseter lateralis superficialis with anterior head distinct, this portion of the muscle not attached to any part of the zygoma except occasionally to a point at extreme base of zygomatic plate; zygomatic plate

tilted upward, usually broad, with its superior border always above lower margin of infraorbital foramen. Infraorbital foramen inferior, transmitting nerve only; masseter lateralis passing obliquely upward to superior border of rostrum, always to exclusion of masseter medialis.

THREE-CUSPED SERIES

Teeth becoming hypsodont on the basis of a tritubercular structure.

Family SCIURIDAE

Skull never truly fossorial; infraorbital foramen with outer wall usually though not always forming a distinct canal, its orifice protected from muscular action by the presence, at or near its lower border, of an outgrowth for attachment of masseter lateralis superficialis; frontal with decurved postorbital process; cheekteeth brachydont or unilaterally hypsodont, the fundamental tritubercular plan usually (probably always) evident in functional adult teeth that have not undergone considerable wear; external form suited to arboreal or terrestrial life.

The *Sciuridae* of authors.

Subfamily *Sciurinae*.—Orbital region normal, the middle of orbit in front of middle of skull (except in genera with greatly elongated rostrum), the lachrymal bone above or in front of anterior extremity of toothrow, the zygomatic plate not especially emarginate below, the postorbital process indicating an evident boundary between orbit and temporal fossa; no parachute membrane.

The entire family except the members of the two following groups; Oligocene to Recent; Northern Hemisphere, South America, continental Africa.

Subfamily *Nannosciurinae*.—Like the *Sciurinae* but orbital region abnormal, the middle of orbit behind middle of skull (rostrum short), the lachrymal bone above middle of toothrow, the zygomatic plate conspicuously emarginate below, the postorbital process not indicating an evident boundary between large orbit and much reduced temporal fossa.

Nannosciurus of the Malay region, *Myosciurus* of West Africa, and *Sciurillus* of South America (the last not seen); Recent.

Subfamily *Pteromyinae*.—Like the *Sciurinae* but with a well developed parachute membrane present.

The Flying-squirrels; Middle Miocene to Recent; Northern Hemisphere.

Family GEOMYIDAE

Skull fossorial; zygoma robust; infraorbital foramen always at end of a long canal, its orifice protected from muscle pressure by counter-

sinking in an oblique sulcus; frontal without postorbital process; cheek-teeth evenly hypsodont or in their extreme development ever-growing, the fundamental tritubercular plan lost in functional adult teeth, the first and second molars of adult consisting of either one or two simple loops. External form in living members of the group highly modified for underground life.

Subfamily *Entoptychinae*.—Angular portion of mandible mostly below alveolar level; cheekteeth rooted, the enamel pattern of first and second molars consisting of two simple loops joined at protomere.²

Entoptychus; North American Oligocene.

Subfamily *Geomyinae*.—Angular portion of mandible mostly above alveolar level; cheekteeth ever-growing, the first and second adult molar consisting each of a simple prism, with an enamel plate always present on anterior surface in upper teeth and on posterior surface of lower teeth.

North American pocket gophers; Miocene to Recent.

Family HETEROMYIDAE

Essential characters as in the *Geomyidae* but skull not fossorial; zygoma slender; orifice of infraorbital canal protected from muscle pressure by countersinking in a vacuity which extends transversely through rostrum; external form murine or saltatorial.

North American pocket-mice and kangaroo-rats; Middle Oligocene (*Heliscomys*) to Recent.

FOUR-CUSPED SERIES

Teeth becoming hypsodont on the basis of a quadritubercular structure.

Family ADJIDAUMIDAE

Zygomasseteric structure³ and infraorbital canal as in the *Sciuridae*; cheekteeth $\frac{4}{4}$, slightly hypsodont, the enamel pattern unmodified heptamerous.⁴

Adjidaumo; North American Middle Oligocene.

² Protomere = inner side of maxillary cheekteeth and outer side of mandibular cheekteeth.

Paramere = outer side of maxillary cheekteeth and inner side of mandibular cheekteeth.

³ Zygomasseteric structure = the combined and correlated structures of the masseter muscle and of the skull in the region at which the muscle takes its origin.

⁴ Heptamerous pattern = the enamel pattern of a flat-crowned cheektooth in which each of seven original tubercles is represented by a loop (two on the protomere, five on the paramere).

Family EUTYPOMYIDAE

Like the *Adjidaumidae* but with cheekteeth somewhat more hypsodont and the heptamorous enamel pattern complicated by the development of a considerable number of secondary closed loops which appear in partially worn teeth as an aggregation of minute enamel lakes covering nearly entire surface of crown.

Eutypomys; North American Middle Oligocene.

Family CHALICOMYIDAE

Like the *Adjidaumidae* but cheekteeth strongly hypsodont and enamel pattern reduced-heptamorous (sometimes paralleling that of the *Hystricidae*) becoming rapidly simplified as the crowns wear away; skull occasionally fossorial; no postorbital process on frontal; no pit-like depression in basioccipital region.

Chalicomys (= *Steneofiber*) and related genera, European Miocene and Pliocene; *Trogontherium*, European Pliocene and Pleistocene; *Palaeocastor*, *Eucastor* and related genera, North American Upper Oligocene and Lower Pliocene.

Family CASTORIDAE

Skull with rostrum broadened and deepened and braincase narrowed; basioccipital region with conspicuous pit-like depression; cheekteeth not ever-growing but so excessively hypsodont that the slightly reduced-heptamorous pattern (parallel: *Myocastor*) changes little with age and rarely if ever wears out; external form highly modified for aquatic life; caudal vertebrae flattened.

Castor; Lower Pliocene to Recent; Northern Hemisphere.

Family CASTOROIDIDAE

Zygomasseteric structure modified by the passage of the shaft of the incisor below the infraorbital foramen instead of above it, the ridge formed by the tooth dividing the area of masseteric origin on side of rostrum into two planes; posterior nares divided horizontally by the median fusing of palatine bones over roots of cheekteeth; teeth ever-growing, the enamel pattern a series of 5-7 parallel transverse ridges (parallel: *Dinomyidae*).

Castoroides; North American Pleistocene.

Superfamily MUROIDAE

Zygomasseteric structure as in the *Sciuroidae* except: Infraorbital foramen superior in whole or in part, entered or traversed by muscle as well as nerve; masseter lateralis seldom reaching superior border of rostrum, and never doing this to exclusion of masseter medialis.

THREE-CUSPED SERIES

Modifications of teeth based on an underlying tritubercular structure.

Family MUSCARDINIDAE

Skull with no striking modifications of general form; zygomatic root, much as in the *Sciuridae* except that its anterior face is nearly vertical instead of strongly oblique, and the infraorbital foramen extends above median level of orbit, receiving or transmitting a strand of muscle as well as the nerve; no postorbital processes; auditory bullae large, globular, rounded in front; cheekteeth $\frac{4}{4}$, brachydont (in *Leithia* subhypodont), the enamel pattern reduced-hexamorous in forms with basin-shaped crowns, passing to a system of parallel transverse ridges in those with flat crowns (parallel: *Graphiuridae*); external form showing a combination of murine and sciurine features.

Eliomys, *Dyromys*, *Glis*, *Muscardinus*, *Leithia*; Old World Middle Miocene to Recent.

FOUR-CUSPED SERIES

Modifications of teeth based on an underlying quadritubercular structure.

Family ISCHYROMYIDAE

General characters of the skull as in the *Muscardinidae*; teeth $\frac{5}{4}$, moderately hypsodont, rooted, the fundamental structure quadritubercular, the enamel pattern in worn teeth reduced-heptamerous.

Ischyromys; North American Middle Oligocene.

Family CRICETIDAE

Fundamental zygomaseteric structure as in the *Muscardinidae* and *Ischyromyidae*, but infraorbital foramen usually enlarged and specialized, consisting of a rounded upper portion for transmission of muscle and a narrow lower portion for transmission of nerve, the zygomatic root developed into a broad, oblique plate; skull varying excessively in form, but always without postorbital process on the frontal; cheekteeth $\frac{3}{3}$, the crown structure showing all stages from brachydont to ever-growing, the fundamental structure quadritubercular, the enamel pattern varying from simple heptamerism to excessive specialization, the tubercles in the maxillary teeth always presenting a longitudinally biserial arrangement and never developing a functional third series on lingual side of crown; external form murine or fossorial.

Subfamily *Cricetinae*.—Skull without special modification, the zygomaseteric structure as usual in the family, the squamosal not developing a postorbital ridge or process; molars rooted, their crowns varying gradually from tubercular and brachydont to flat-crowned and strongly hypsodont, when in the latter condition the prisms not opposite (compare *Gerbillinae*) and the posterior termination of m^1 and m^2 not angular (compare *Microtinae*).

The *Cricetinae*, *Sigmodontinae*, *Neotominae*, and *Nesomyinae* of authors; Oligocene to Recent; continental region of the world; Madagascar.

Subfamily *Gerbillinae*.—Auditory bullae and entire posterior portion of skull enlarged; teeth subhypsodont or hypsodont, flat-crowned in adults, with opposite prisms, these tending to form transverse ridges joined at median line, or, in their extreme development, to separate into plates; external form saltatorial.

The *Gerbillinae* of authors; Recent only, unless *Trilophomys* from the Pliocene of France is a member of the group; Asia and Africa.

Subfamily *Microtinae*.—Like the more hypsodont members of the subfamily *Cricetinae* but cheekteeth often growing from a persistent pulp, the enamel pattern always consisting of (at least partially) alternating triangles, the posterior termination of m^1 and m^2 never rounded; squamosal with distinct postorbital ridge or process.

The *Microtinae* of authors; Miocene to Recent; Northern Hemisphere.

Subfamily *Lophiomyinae*.—Like the *Cricetinae* with tubercular, slightly hypsodont teeth, but skull with temporal fossa bridged by a plate formed of laminae arising from the jugal, frontal, and parietal, a structure not known to occur elsewhere among rodents.

Lophiomyis; Recent; Africa.

Family PLATACANTHOMYIDAE

Like the *Cricetidae* but zygomaseteric structure unusual, the infraorbital foramen of normal cricetine form, but zygomatic plate much narrowed, and masseter lateralis profundus extending its line of attachment along upper zygomatic border to side of rostrum above foramen; cheekteeth subhypsodont, the enamel pattern a modified heptamerous with tendency to form parallel oblique cross-ridges (parallel: *Muscardinidae*).

Platacanthomys and *Typhlomys*; Recent; Southern Asia.

Family RHIZOMYIDAE

Like the *Cricetidae* but zygomaseteric structure unusual, the infraorbital foramen with neural portion reduced or obliterated by partial or entire fusion of zygomatic plate with side of rostrum; skull and external form fossorial.

Subfamily *Tachyoryctinae*.—Infraorbital foramen with neural portion reduced to an inconspicuous notch by fusion of the broad zygomatic plate with side of rostrum (outline of plate below foramen usually visible); skull strongly fossorial; cheekteeth closed at base but extremely hypsodont, the enamel pattern not changing in character during adult life; enamel pattern in adult consisting of 2-3 parallel curved cross-ridges (the concave surface directed backward and outward in upper teeth, forward and inward in lower teeth; parallel: *Protechimys*); reduced-heptamerism evident in unworn enamel cap; external form modified, though not excessively, for underground life.

Tachyoryctes; Recent; Africa.

Subfamily *Rhizomyinae*.—Like the *Tachyoryctinae* but peculiarities of infraorbital region carried farther, the neural notch being obliterated and the foramen appearing as a small orifice confined to upper surface of zygomatic root; teeth moderately hypsodont, the enamel pattern obviously heptamerous or reduced-heptamerous and changing rapidly during adult life.

Rhizomys and related genera; Pliocene to Recent; southern Asia.

Subfamily *Braminae*.—Like the *Rhizomyinae* but cheekteeth with definitely prismatic structure.

Bramus; Pleistocene; northern Africa (not seen).

Family SPALACIDAE

Like the *Cricetidae* but zygomaseteric structure unusual, the zygomatic plate narrowed and turned downward to a nearly horizontal position, thus doing away with the separate neural portion of the opening by a process the exact opposite to that bringing about a similar result in some of the *Rhizomyidae*; skull excessively fossorial, the lambdoid crest carried forward to level of zygomatic root.

Subfamily *Myospalacinae*.—Mandible scarcely movable at symphysis, a large post-symphyseal buttress early developed; cheekteeth growing from persistent pulps, the crowns elongated, the enamel pattern consisting of alternating triangles, the posterior termination of m^1 and m^2 rounded.

Myospalax; Recent; Asia.

Subfamily *Spalacinae*.—Mandible movable at symphysis throughout life; cheekteeth moderately hypsodont, rooted, subterete, the pattern reduced-heptamerous, changing rapidly with wear; skull with the characters of the family carried to such an extreme as to make it the most fossorial type known among rodents.

Spalax, Recent, *Prospalax*, Upper Pliocene, and an undescribed genus from the upper Oligocene; eastern Mediterranean Region, and southern Europe.

Family MURIDAE

Skull as in the typical *Cricetidae*; cheekteeth $\frac{3}{3}$, the upper teeth with a functional row of tubercles on lingual side of crown internal to the protocone and hypocone, these tubercles entering conspicuously into the plan of modification of the crowns.

Subfamily *Dendromyinae*.—Upper cheekteeth with triserial arrangement not fully developed; manus with only 3 functional digits.

The *Dendromyinae* of authors; Recent; Africa.

Subfamily *Murinae*.—Upper cheekteeth with fully developed triserial arrangement of tubercles always evident, though frequently vary-

ing from the symmetrical plan; crowns brachydont or slightly hypsodont; manus normal.

The *Murinae* of authors; Upper Miocene to Recent; Old World, except Madagascar.

Subfamily *Phloeomyinae*.—Upper cheekteeth with triserial arrangement of elements obscured by flattening out of each trio of tubercles to form a simple, detached, transverse lamina (parallel: *Diplomys*); crowns moderately hypsodont; braincase relatively small and auditory bullae reduced; external form heavy, arboreal.

Phloeomys; Recent; Philippine Islands.

Subfamily *Otomyinae*.—Upper cheekteeth with same modification as in the *Phloeomyinae*, but m^3 tending to become the dominant tooth in the series, its size always greater than that of m^2 , and its elements usually reduplicated; external form heavy, terrestrial.

Otomys; Recent; Africa.

Subfamily *Hydromyinae*.—Upper cheekteeth with triserial arrangement obscured by suppression of tubercles of outer series; m^3 vestigial.

The *Hydromyinae* of authors; Recent; Australian Region.

Superfamily DIPODOIDAE

Masseter lateralis superficialis with anterior head not distinct, this portion of the muscle attaching along a considerable area on anterior border of zygoma; zygomatic plate nearly horizontal, always narrow and completely beneath infraorbital foramen. Angular portion of mandible not distorted outward at base to permit free passage of a branch of the masseter lateralis, its general direction not parallel with zygoma.

THREE-CUSPED SERIES

Modifications of teeth based on an underlying tritubercular structure, the hypocone when present not entering into the essential mechanical scheme of the crown.

A.—Skull with no special peculiarities except that the auditory bullae appear to be imperfect or absent (perhaps merely reduced as in *Phloeomys*); infraorbital foramen not transmitting muscle; cheekteeth brachydont or subhypsodont, their structure essentially as in the less modified *Sciuridae*.

Family PARAMYIDAE

Rostrum and braincase approximately equal in width, infraorbital foramen very small, not visible in lateral view of the skull; cheekteeth $\frac{5}{4}$, the upper molars obviously and simply tritubercular in general plan, the hypocone, when present, appearing as a supplement to the original structure of the tooth.

Paramys, *Mysops*, *Prosciurus*, and related genera; North American Lower Eocene to Middle Oligocene.

B.—Skull and teeth as in the *Paramyids* except that the auditory bullae are well developed, the infraorbital foramen is enlarged to transmit a small strand of muscle, and the cheekteeth are flattened.

Family GRAPHIURIDAE

Cheekteeth $\frac{3}{4}$, brachydont, crowns wider than long, basin-shaped with small tubercles and low ridges (parallel: *Muscardinidae*); skull with no special peculiarities, the braincase much wider than rostrum; auditory bullae globular; external form muscardinine.

Graphiurus; Recent; Africa.

C.—Skull fossorial (except perhaps in the *Allomyidae*); infraorbital foramen not transmitting muscle; auditory bullae well-developed; cheekteeth brachydont, hypsodont, or ever-growing; modification of crowns based on a structure including well developed protoconule and metaconule, and conspicuously trenchant outer commissures.

Family ALLOMYIDAE

Cheekteeth $\frac{5}{4}$, brachydont or moderately hypsodont, the tritubercular structure of upper teeth evident in unworn crowns; protoconule and metaconule large; functional cusps in m^1 and m^2 ; mesostyle appearing in hypsodont forms as a conspicuous median rib on outer surface of crown (parallel: *Pseudosciuridae*).

Allomys, *Haplomys*,⁵ *Meniscomys*, *Mylagaulodon*; North American Upper Oligocene and Miocene.

Family APLODONTIIDAE

Like the *Allomyidae* but the skull greatly widened posteriorly, the auditory bullae flask-shaped with neck directed horizontally outward; cheekteeth growing from persistent pulp, the unworn caps showing evident pattern of the *Allomys*-type, this soon wearing away and leaving a simple enamel ring; paramere with conspicuous vertical ridge.

Aplodontia; Pleistocene and Recent; *Liodontia*,⁶ Miocene; western North America.

Family CYLINDRODONTIDAE

Skull fossorial with braincase slightly wider than rostrum; cheekteeth $\frac{3}{4}$, subterete, excessively hypsodont but not growing from persistent pulp, the enamel pattern in considerably worn upper teeth consisting of an outer ring and a central lake.

Cylindrodont; North American Lower Oligocene. Position of group doubtful.

⁵ New genus, type *Meniscomys liolophus* Cope.

⁶ New genus, type *Aplodontia alexandrae* Furlong.

FOUR-CUSPED SERIES

Modifications of teeth based on an underlying quadritubercular structure, the hypocone always entering into the essential mechanical scheme of the crown.

A.—Skull not specially modified; upper molars with large protoconule and metaconule, and conspicuously trenchant outer commissures, their structure paralleling that of the *Allomyidae* in the three-cusped series.

Family PSEUDOSCIURIDAE

Skull essentially as in the *Sciuravidae* but with larger infraorbital foramen which may have transmitted a strand of muscle.

Pseudosciurus; European Oligocene.

B.—Skull excessively fossorial; occipital region obliquely truncate, with lambdoid crest moved forward nearly to level of zygomatic root; frontal with short postorbital process; bony horn-cores present on rostrum in two genera, absent in a third; cheekteeth highly modified from a normal heptamerous structure, the grinding function of toothrow in adult almost completely taken over by the greatly enlarged fourth premolar.

Family MYLAGAULIDAE

General structure of skull much as in the *Aplodontiidae*; cheekteeth $\frac{4}{4}$ or $\frac{3}{3}$; a reduced-heptamerous pattern evident in slightly worn crowns, but this giving place with wear to a system of narrow longitudinal and oblique lakes; molars relatively small, soon crowded out by the premolar, an excessively hypsodont, laterally compressed tooth, closed at the base, and rapidly increasing in crown length from the unworn surface downward. Skeleton highly modified for underground life.

Mylagaulus, *Ceratogaulus*, and *Epigaulus*; North American Miocene and Pliocene.

C.—Skull without special peculiarities; infraorbital foramen moderate or very large, transmitting both muscle and nerve; cheekteeth subhypsodont or brachydont, their modifications based on a heptamerous structure in which the ridges are narrow and the reentrant spaces wide (parallels: *Funisciurus*, *Erethizontidae*); external form glirine or pteromyine; under side of tail with scaly outgrowths near base.

Family ANOMALURIDAE

Skull with moderate infraorbital foramen; lower zygomatic root at level immediately in front of anterior cheektooth; anterior point of masseteric insertion on mandible beneath hinder part of m_1 ; no discrepancy between size of incisors and molars; cheekteeth subhypsodont, their crowns flat, longer than wide; external form pteromyine.

Anomalurus; Recent; Africa.

Family IDIURIDAE

Like the *Anomaluridae* but skull with infraorbital foramen greatly enlarged, the lower zygomatic root nearer to incisor than to anterior cheektooth; anterior point of masseteric insertion on mandible in front of pm^4 ; incisors excessively heavy; cheekteeth weak, extremely brachydont, their crowns flat, wider than long.

Subfamily *Idiurinae*.—Flying membrane present; cheekteeth with two complete median transverse ridges.

Idiurus; Recent; Africa.

Subfamily *Zenkerellinae*.—Flying-membrane absent; cheekteeth with one complete median transverse ridge.

Zenkerella; Recent; Africa.

D.—*Skull without striking peculiarities other than a tendency to assume a form characterized by broad braincase, large auditory parts, and weak rostrum (parallels; Gerbillinae, Octodontinae); infraorbital foramen transmitting muscle in all members of the group in which the skull is known except probably Sciuravus; cheekteeth varying from brachydont to ever-growing, their modifications based on a heptamerous structure in which the ridges are wide and the reentrant spaces narrow.*

Family SCIURAVIDAE

Infraorbital foramen small, but visible in lateral view of skull, probably transmitting nerve only; cheekteeth $\frac{5}{4}$, brachydont; the structure of the upper molars obviously and simply quadritubercular.

Sciuravus; North American Middle Eocene.

Family ZAPODIDAE

Infraorbital foramen large, transmitting muscle as well as nerve; cheekteeth varying in number from $\frac{5}{4}$ in the earlier members of the group to $\frac{3}{2}$ in the most advanced; the quadritubercular crown structure usually though not always much modified; metatarsals not reduced or fused.

Subfamily *Theridomyinae*.—The earlier, less modified members of the family: pm^4 a large, functional tooth; crowns of cheekteeth varying from brachydont and simply quadritubercular (*Sciuroides*) to hypsodont and much reduced heptamerous (*Issiodoromys*; parallel: *Eocardia*).

The *Theridomyidae* of authors; European Lower Eocene to Miocene.

Subfamily *Sicistinae*.—Cheekteeth brachydont, $\frac{4}{3}$, distinctly quadrituberculate, the enamel of moderately worn upper molars with a simple heptamerous pattern; external form murine, the hind legs and feet not lengthened.

Sicista, Recent, Eurasia; ? *Eomys*, European Upper Eocene.

Subfamily *Zapodinae*.—Cheekteeth subhypso-dont, $\frac{4}{3}$ or $\frac{3}{3}$, flat crowned, the enamel pattern of the upper molars heptamorous, slightly or considerably modified; external form saltatorial, the hind legs and feet lengthened.

Eozapus, Recent, China; *Zapus*, *Napaeozapus*, Pleistocene and Recent, North America.

Family DIPODIDAE

Like the *Zapodidae* but with the inner and outer metatarsals reduced or absent and the three median fused to form a canon bone; cheekteeth hypso-dont, the heptamorous enamel pattern undergoing modifications most of which are parallel to those taking place in the teeth of the *Cricetidae* and in the hystricine families.

Subfamily *Protoptychinae*.—Upper cheekteeth 4, moderately hypso-dont; pm⁴ a large, functional tooth; skull with relatively broad rostrum and narrow braincase.

Protoptychus,⁷ North American Upper Eocene.

Subfamily *Dipodinae*.—Cheekteeth $\frac{4}{3}$ or $\frac{3}{3}$, strongly hypso-dont; pm⁴ vestigial; skull with relatively narrow rostrum and broad braincase.

The *Dipodidae* of authors who recognize the *Zapodidae* as a distinct family; Pleistocene and Recent; Eurasia and northern Africa.

Family CTENODACTYLIDAE

Cheekteeth growing from a persistent pulp, the adult pattern reduced to a simple ring infolded on one or both sides (parallel: *Octodontinae*); external form fossorial.

Ctenodactylus and related genera from the Mediterranean region; Pliocene to Recent.

Family PEDETIDAE

Cheekteeth subterete, growing from a persistent pulp; all trace of the original crown structure lost, the unworn enamel cap transversely cleft, the adult pattern consisting of a narrow median infold from the paramere extending nearly across to opposite side; external form conspicuously saltatorial, but median metatarsals showing no tendency to become reduced or fused.

Pedetes; Recent; Africa.

Superfamily BATHYERGOIDAE

Zygomasseteric structure as in the *Dipodoidae* except: Angular portion of mandible distorted outward to allow passage of a specialized and

⁷ While *Protoptychus* is a true dipodid with few primitive characters its exact position is not clear. It may prove to be a member of the *Theridomyinae*; but for the present we prefer to place it in the *Dipodidae* on account of its resemblance to the recent genus *Euchoreutes*.

enlarged distal anterior limb of the masseter lateralis superficialis, its general direction parallel with zygoma. Masseter medialis arising from upper margin of orbit and not passing through small infraorbital foramen.

Family BATHYERGIDAE

Skull and external form with conspicuous fossorial adaptations. Cheekteeth extremely hypsodont, though not ever-growing; enamel pattern in adult a ring with or without a reentrant fold on one or each side (parallel: *Octodontinae*); number of cheekteeth ranging from $\frac{2}{2}$ to $\frac{6}{6}$. (In the genus, *Heliophobius*, with the greatest number of teeth there are never more than $\frac{5}{4}$ functional at one time; the apparent addition of one tooth in the upper jaw and two in the lower jaw to the maximum rodent formula is probably due to a specialized condition of the milk dentition.)

The *Bathyergidae* of authors; Recent; Africa.

Superfamily HYSTRICOIDAE

Zygomasseteric structure as in the *Bathyergoidae* except: Masseter medialis arising from side of rostrum and passing through large infra-orbital foramen.

LATERALIS SERIES

Masseter lateralis the chief agent in modifying form of outer side of mandible; an oblique ridge extending forward from lower border of angular process usually present for attachment of this muscle.

A.—*Lachrymal bone small, forming no important part of zygomatic root, its lower portion confined within orbit; lachrymal canal closed in front of orbit.*

Family HYSTRICIDAE

Skull with no special peculiarities other than a tendency (most pronounced in the genus *Hystrix*) to inflation of the rostral and frontal regions; mandibular rami rather freely movable at symphysis; angular process deep, neither produced backward conspicuously behind articular level nor folded inward along lower margin; cheekteeth $\frac{4}{4}$, their enamel pattern slightly removed from the simple heptamerous type, the reentrant folds narrow and not angular.

Old World porcupines; Upper Miocene to Recent.

Subfamily *Hystriinae*.—Base of upper zygomatic root over a point decidedly behind the anterior extremity of toothrow; cheekteeth strongly hypsodont, closed at base but without definite roots; sacral vertebrae 4.

Hystrix, *Acanthion*, *Thecurus*; Africa, southern Asia, and Malay region.

Subfamily *Atherurinae*.—Base of upper zygomatic root over anterior extremity of toothrow; cheekteeth subhypsodont, with well developed roots; sacral vertebrae 3.

Atherurus, *Trichys*: Recent; Malay region.

Family ERETHIZONTIDAE

Like the *Hystriidae* but: Mandibular rami with conspicuous post-symphyseal buttresses which prevent movement at the symphysis; lower border of angular process folded inward; cheekteeth subhypsodont, flat crowned, with reduced-heptamerous enamel pattern characterized by narrow ridges and wide reentrant spaces, the spaces on the paramere tending to become transformed into pits (parallels: *Funisciurus*, *Anomaluridae*). Upper zygomatic root over anterior part of toothrow; feet noticeably modified for arboreal life.

New World porcupines except *Chaetomys*: Oligocene to Recent. Oligocene of Egypt?⁸ Extinct South American genera: *Asteromys*, *Eosteiomys*, *Parasteiomys*, *Steiromys*.

Family ECHIMYIDAE

Like the *Erethizontidae* but lower border of angular process usually with no evident infolding, feet usually not modified for arboreal life, and adult cheekteeth with narrow reentrant folds; cheekteeth varying from brachydont to ever-growing, the structure when hypsodont not multilaminar.

Subfamily *Echimyinae*.—Fossorial specialization usually absent; skull and cheekteeth showing great variety of form; enamel pattern not simplified to a ring with an infold on one or each side.

Tropical America; Miocene to Recent. Spiny-rats (provisionally including *Chaetomys*), Hutias (*Capromys*, *Plagiodontia*), etc.; also many extinct genera, among them *Acaremys*, *Boromys*, *Brotomys*, *Colpostemma*, *Eocardia* (parallel: *Issiodoromys*), *Eoetodon*, *Graphimys*, *Gyrignophus*, *Haplostropha*, *Heteropsomys*, *Homopsomys*, *Isolobodon*, *Prospaniomys*, *Protadelphomys*, *Protacaremys*, *Sciamys*, *Scleromys*, *Spaniomys*, *Stichomys*, *Strophostephanus*, *Tribodon*. It is probable that this group needs subdividing.

Subfamily *Octodontinae*.—Fossorial specialization usually present; cheekteeth, except in earliest known genera, with enamel pattern completely simplified to a ring with an infold on one or each side (parallel: *Ctenodactylidae*).

South America; Oligocene to Recent. Recent genera: *Ctenomys*, *Octodon*, *Octodontomys*, *Spalacopus*. Among the fossil genera are: *Cephalomys*, *Dicoelophorus*, *Eucoelophorus*, *Litodontomys*, *Neophanomys*, *Palaeoctodon*, *Phthoramys*, *Pithanotomys*, *Plataeomys*, *Scotomys*.

⁸ The genera *Phiomys* and *Metaphiomys*, based on lower jaws and teeth, have no characters by which they can at present be referred to any other family.

Family PETROMYIDAE

In general resembling the *Octodontinae* but crown of each cheektooth margined by two elevations on the protomere, these elevations probably resulting from the unusual obliquity at which the teeth appear to be set. The teeth are rooted, strongly hypsodont; the enamel pattern consists of two transverse lobes united by a median isthmus, the outer edges of the lobes becoming joined in the upper teeth when worn. No specimens examined.⁹ Recognized as a family by Tullberg, partly on whose authority we continue to treat it as distinct. The characters of the teeth indicate important mechanical peculiarities of the chewing apparatus. The enamel pattern appears to be of a type which could be directly derived from that present in the relatively low-crowned molars of *Erethizon* and the Oligocene African *Phiomys*.

Petromys, South Africa: Recent.

Family MYOCASTORIDAE

In general like the *Erethizontidae* but upper zygomatic root over middle of toothrow, and cheekteeth with structure paralleling that present in *Castor*; lateral process of paroccipital large, projecting freely above base of greatly elongated paroccipital process; in living species external form modified for aquatic life.

Myocastor and related fossil genera; South America; Miocene to Recent.

Family THRYONOMYIDAE

Like the *Myocastoridae* but cheekteeth with structure paralleling that present in some of the *Echimyinae*, and lateral process of paroccipital small, closely applied to base of moderately large paroccipital process; external form not modified for aquatic life.

Thryonomys; Africa; Recent.

Family DINOMYIDAE

Like the *Echimyidae* but cheekteeth combining a multilaminar structure with excessive hypsodonty (parallel: *Castoroides*); so far as known the external form is robust, terrestrial.

South America and the Greater Antilles; Miocene to Recent. Includes the living *Dinomys* and the extinct genera *Amblyrhiza*, *Briaromys*, *Discolomys*, *Elasmodontomys*, *Gyriabrus*, *Megamys*, *Neoeplema*, *Olenopsis*, *Potamarchus*, *Tetrastylus*.

Family CUNICULIDAE

Not essentially different from the *Dinomyidae*, but the jugal and part of the maxillary are expanded to form a conspicuous cheekplate, the surface of this becoming excessively rugose in adult; cheekteeth strongly

⁹ Mr. Oldfield Thomas has kindly sent us photographs of a skull in the British Museum (No. 4.2.3.98).

hypsodont, but enamel structure not completely multilaminar; external form robust, terrestrial.

Cuniculus (= "*Coelogenys*"); Tropical America; Pleistocene and Recent.

Family HEPTAXODONTIDAE

First tooth of maxillary series mechanically dominant, cheekteeth apparently reduced to $\frac{2}{3}$, conditions not known elsewhere in the *Hystrioidae*, and indicating zygomaseteric development along a line different from that followed elsewhere in the group; enamel structure multilaminar with reduplication in the anterior tooth; diagnostic cranial characters unknown.

Heptaxodon; Porto Rico; Pleistocene? The genus *Morenia* from the South American Miocene may be a second member of the family; it is at present known from isolated teeth only.

B.—*Lachrymal bone large, usually forming an important part of zygomatic root, its lower portion extending forward out of orbit to a level in front of anterior margin of infraorbital foramen; some part of lachrymal canal open on side of rostrum in front of orbit.*

Family DASYPROCTIDAE

Skull generalized in structure, closely resembling that of the less specialized *Hystrioidae*; cheekteeth hypsodont but with a nearly unmodified heptamerous structure, paralleling that in the *Hystrioidae*; external form cursorial, the legs lengthened, the digits 5–3.¹⁰

The *Dasyproctidae* of authors with *Cuniculus* removed and *Neoromys* added; South and Middle America; Miocene to Recent.

Family CHINCHILLIDAE

Cheekteeth with heptamerous structure excessively modified, the enamel pattern consisting of parallel transverse laminae (parallel: *Dinomyidae*); mandible with no sharply defined ridge for attachment of masseter lateralis; external form saltatorial.

South America; Miocene to Recent. Living genera: *Chinchilla*, *Lagostomus*, *Viscaccia*. Extinct genera: *Euphilus*, *Perimys*, *Pliolagostomus*, *Prolagostomus*, *Scotaëumys*, *Sphaeromys*.

Family ABROCOMIDAE

Like the *Chinchillidae* but cheekteeth with deep reentrant angles on both sides, and mandible with sharply defined ridge for attachment of masseter lateralis; external form not saltatorial.

Abrocoma; South America; Pliocene to Recent.

¹⁰ The feet of *Neoromys* are imperfectly known, but there appears to be nothing in the structure of the parts which have been described that indicates the presence of more than three digits in the hind foot.

MEDIALIS SERIES

Masseter medialis the chief agent in modifying form of outer side of mandible; a conspicuous horizontal ridge for the attachment of this muscle present on side of mandible slightly below alveolar level.

Family CAVIIDAE

Posterior cheektooth both above and below without reduplication of elements, the general character of the toothrow normal.

The *Caviidae* of authors with *Hydrochoerus* and its allies removed; South America; Miocene to Recent. Extinct genera: *Anchimys*, *Neoprocavia*, *Orthomyctera*, *Palaeocavia*, *Phugatherium*, *Procardiotherium*.

Family HYDROCHOERIDAE

Posterior cheektooth both above and below with conspicuous reduplication of elements, the general character of the toothrow thus rendered abnormal.

Hydrochoerus and its extinct allies *Plexochoerus*, *Prohydrochoerus* and *Protohydrochoerus*; perhaps *Cardiomys*, *Caviodon* (= *Diocartherium*) and *Cardiotherium* also; South America, Miocene to Recent; southeastern United States, Pleistocene.